

ABSTRACT

The quantitative impact on internal plant nutrient transport in a leaf-eating insect (*Dasychira pudibunda* L.) in southern Sweden, caused by defoliation by the larvae of the pine sawfly (*Neodiprion pini* L.) and the European spruce sawfly (*Pristiphora excelsa* L.) was studied in 1975-1977. No significant differences in 1975, a partial defoliation took place in 1976, and a total one in 1977. Total annual litter fall was similar during the three years however.

Leaf litter fall was 3.0, 3.1 and 3.5 t/ha in 1975, 1976 and 1977, respectively. In 1977 17% of the litter was of *D. pudibunda* origin. In 1976 and 1977, the litter was of *D. pudibunda* and *P. excelsa* origin, respectively.

The transport of N, P and K in total stems per ha was 100 kg in 1975 and 1977, but significantly lower in 1976.

THE INFLUENCE OF A LEAF-EATING INSECT (*DASYCHIRA PUDIBUNDA* L. LEPIDOPTERA) ON INTERNAL PLANT NUTRIENT TRANSPORTS AND TREE GROWTH IN A BEECH FOREST (*FAGUS SYLVATICA* L.) IN SOUTHERN SWEDEN

Years are given for above-ground litter transport in kg/ha and nutrient transport in kg/ha.

- 1) Litter fall from damaged and undamaged leaves.
- 2) Litter fall from damaged leaves.
- 3) The contribution of *Dasychira* to total litter fall.

Tree growth was measured in beech stands in 1975, 1976 and 1977. The stands were defoliated during two years. No growth reduction could be attributed to leaf consumption and litter fall.

The population ecology of the pine sawfly is reviewed from the available literature, and some hypotheses are put forward concerning the population and adaptive strategies of the pine and beech populations.

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ABSTRACT

The quantitative impact on internal plant nutrient transport in a beech stand (*Fagus sylvatica* L.) in southern Sweden, caused by defoliation by the larvae of the pale tussock moth (*Dasychira pudibunda* L. Lepidoptera) was studied 1971-1973. No defoliation occurred in 1971, a partial defoliation took place in 1972, and a total one in 1973. Total annual litter fall was similar during the three years, however.

Leaf litter fall was 3.01 ± 0.13 ; 2.58 ± 0.13 and 0.79 ± 0.04 ton.ha⁻¹ year⁻¹ respectively. In 1973 17.0, 29.6, 9.0 and 6.4% of total litterfall consisted of leaves, larval faeces, bud scales and acorns respectively.

The transport of N, P and K in total litter fall was fairly similar in 1971 and 1973, but throughfall transport of the same elements increased about three times in 1973, compared to 1971.

The contents of S, Cu, Mn, Ca, Mg and Na were also measured in litter fall. Significant differences between years are found for these elements. Differences in plant nutrient fluxes are related to:

- 1) Leaching from faeces and injured leaves.
- 2) Time of peak litter fall.
- 3) The contribution of faeces to total litter fall.

Stem growth was measured on felled logs, emanating from trees that were defoliated during two years. No growth reduction which could be clearly attributed to leaf consumption was found.

The population ecology of the pale tussock moth is surveyed from the available literature, and some hypotheses are put forward concerning the coevolution and adaptive strategies of the moth and beech populations.

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1 INTRODUCTION

The major pathway for energy flow and plant nutrient fluxes in terrestrial ecosystems runs from the primary producers to the decomposer organisms in the soil. The food chain plants - herbivores - carnivores is quantitatively much less important in this respect (cf. compilations in Odum 1971 and McNaughton and Wolf 1973). A simulation model described by Lee and Inman (1975) seemed to indicate that herbivores level out fluctuations in primary production, probably because of selective grazing of e.g. current shoots including reproductive organs. This reasoning is only valid for ecosystems that are relatively unaffected by the activities of man. It is obvious that in e.g. pastures and rangelands which are heavily grazed by cattle, the fluxes of energy and nutrients between plants and herbivores become quantitatively more important.

In a forest ecosystem litter emanating from above ground plant parts is the major carrying substance of energy and nutrients to the soil decomposer compartment. Due to the activities of decomposer organisms plant nutrients are released and/or mineralized to a form available for root uptake. Mineralization is distinguished as a biological process, while release is purely physical in nature, e.g. the release of cell vacuole potassium due to mechanical destruction of the cell walls.

Plant nutrients from outside the ecosystem are transported principally by atmospheric dry and wet deposition. The chemical composition of wet deposition (incident rainfall), is drastically changed, when the water is passing through the tree canopy. There is an overall plant nutrient enrichment due to: 1) Solvation of dry deposited material on leaves and branches; 2) Plant nutrients are leached from senescent leaves, bark and bark epiphytes. The precipitation reaching the ground is commonly divided into two qualitatively and quantitatively differing fractions:

- 1) Throughfall precipitation, which is passing either directly to the ground or via leaves and twigs.

- 2) Stemflow precipitation, which is passing via large branches and the tree trunks (cf e.g. Carlisle et al 1966b, 1967, Mayer 1971, Nihlgård 1971, Nilsson 1973).

Stemflow is usually the minor of the two fractions, but has the highest plant nutrient concentration.

The main questions that will be asked in this paper are the following ones:

- 1) In what ways can an outburst of a leaf-eating insect population affect
 - a) the transport of plant nutrients by stand precipitation to the soil compartment,
 - b) the transport of organic matter (energy) and mineralizable and/or releasable plant nutrients by litter fall to the soil compartment.
- 2) Does the leaf consumption affect tree growth?
- 3) Which is the coevolutionary implication for an insect and a tree population caused by wild fluctuations of the former population?

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2 INVESTIGATION AREA

Field studies were performed in Kongalund, a 90-year-old beech forest (*Fagus sylvatica* L.) situated at the southern slope of the Archaean ridge of Söderåsen (55°59'N, 13°10'E). The bedrock consists of Cambrian shales and sandstones, which are overlaid by a thick layer of glacifluvial moraine with a fairly even distribution of grain sizes (Nihlgård 1971), the sand being the dominating fraction within the research plot used by the present author (locality 17 according to Nilsson 1977). The soil is an acid brown earth (Nihlgård 1971, Nilsson 1977). Mean annual temperature is 6-7°C (Atlas över Sverige 1953). The yearly precipitation is 800 mm, the humidity being 270 mm (Tamm 1959). The beech forest should be classified as belonging to the *Lamium galeobdolon* type L. with *Stellaria nemorum* ssp *glochidosperma* L. as a codominating species in the field layer (classification according to Lindgren 1970).

Tab. 1 shows some stand data compared with those given by Nihlgård (1972) from another research plot in the same general area.

3 PATTERNS OF LEAF CONSUMPTION AND THE POPULATION ECOLOGY OF THE PALE TUSSOCK MOTHS (*DASYCHIRA PUDIBUNDA* L. LEPIDOPTERA)

During 1972 large parts of the beech forest were invaded during July and August by a fast growing population of *Dasychira pudibunda* larvae, (abbreviated as D.p. in the following text).

Many trees were completely defoliated, although the trees belonging to the research plot were only slightly affected. During 1973 the whole beech forest was defoliated (ca. 15 ha).

The biology of D.p. in Sweden has been studied mainly by Heqvist (1946) and Sylvé (1942, 1943). Notes about the occurrence of the species in beech forests outside Sweden are found in inter alia Kruel (1958) for G.D.R. and Ritzema (1914) for the Netherlands. Rafes (1970) cites investigations on oak leaf consumption by D.p. in the USSR. According to compilations made by Heqvist (1946), the larvae can utilize a large array of species including raspberry (*Rubus idaeus* L.), the leaf consumption of which was clearly visible in the Kongalund forest. Beech is usually preferred however. The studies by Sylvé (1943) were performed in 1941 and 1942 in the same general area as the present investigation during a peak in population number. According to him adult insects have their flying period during May and June. Pupae thus hatch in May. Mating takes place immediately after hatching, followed by the egg-laying of the females.

Egg-hatching takes place three weeks later. Even the youngest larvae possess an excellent moving ability, either by creeping or by spinning strong threads with the help of which climbing up and down the tree stems becomes fairly easy. The use of threads is restricted to instars no 1-3. The later instars become too heavy for this kind of activity. Positive phototropism is shown by all larval stages.

At the end of September food intake ceases and the larvae head for the ground and pupate in the leaf litter layer.

Both larvae and pupae are attacked by a large number of parasites and predators, such as the fungus *Cordyceps militaris* Fr. and various insect species belonging to the Ichneumonidae family, Hymenoptera (Sylvén 1942, 1943). Virus infections are described by e.g. Orlovskaya (1968).

According to the available literature and own observations the population peaks seem to occur during a two-year-period with an interval of 20-30 years between the periods. A simulation model which might be appropriate in this context was presented by Myers (1976) based on investigation data given by Monro (1967).

Density dependent dispersal, i.e. migration from plants which are heavily utilized, combined with a high survival rate of migrating individuals should, according to the model destabilize and diminish population size rather rapidly probably due to an effective overexploitation of the food resource. Populations with this kind of behaviour are regarded "K unresponsive" (cf. Mc Naughton & Wolf 1973), i.e. they "do not know" the size of the environment's carrying capacity. The growth of such populations can be described by a J-shaped curve, i.e. a rapidly occurring maximum followed by a rapid decline.

The D.p. population seems to behave at least to some extent according to the presented model. In the present study the food resource was not fully exploited during 1972 but became so during the following year, followed by a rapid population decline in 1974. The importance of parasites and predators should be stressed, however. The evolutionary implications of oscillating population numbers will be discussed later.

4 FIELD METHODS

The research plot consisted of a square 50 x 50 m, adjacent to a 70-year-old spruce plantation.

20 rain water gauges consisting of plastic bottles equipped with plastic funnels (200 cm^2) were randomly placed within the plot. A piece of glass wool was put into the neck of the funnel to prevent contamination by dust, insects etc. The upper edge of the funnel was situated 30 cm above ground level. Each gauge was placed inside a metal tube which was dug into the ground. Three rain water gauges of the same construction were placed in an open field and were used for the comparison between incident rainfall and stand precipitation. All gauges were emptied at the same time intervals, usually once a week. Chemical analyses were usually performed on pooled samples. Analyses of individual samples were made occasionally, however, during different seasons of the year to check the spatial variation. Fifteen litter traps consisting of a terylene mesh bag suspended from an aluminium hoop were randomly placed within the plot. The aluminium hoop was situated one metre above the ground and had an upper width of 0.25 m^2 . Litter sampling was performed at irregular time intervals, usually once a month during the period of November to September and once a week during peak litter fall (October - early November). 1973 forms an exception to this scheme for reasons given above.

0.15% and 0.02% of the investigation plot was thus covered by litter traps and rain water gauges respectively.

5 LABORATORY METHODS

Stand precipitation was measured volumetrically and converted to litre $\cdot m^{-2}$ (mm). Samples were pooled and stored at a temperature of 4-6°C. PO_4 -P was analysed within one week, the rest of the analyses being performed within one month.

PO_4 -P: according to Murphy and Riley (1962).

Total N (NH_4^+ + NO_3^- + org. N):

- 1) According to Egner, Brodin & Johansson (1955), using Nessler's reagent and Devarda's alloy as complex forming reagent and nitrate reduction agent, respectively.
- 2) The same as above but using indophenol blue as complex forming reagent mainly according to Hoffmann and Teicher (1962). The two methods show good correspondence.

K: Flame emission.

Litter was sorted into leaves, twigs and "other litter". Bud scales, acorns and faeces were treated as separate fractions during 1973, and on some sampling occasions during 1971 and 1972. The sorted litter was dried at 85°C for 48 hours and put into plastic bags which were carefully sealed to avoid contamination.

The samples were ground in a mill prior to analysis. 1.000 g was digested (duplicate samples) with a mixture consisting of conc. HNO_3 and conc. $HClO_4$ (volume ratio 4:1), according to Johnson and Ulrich (1960). 2-3 blanks were run together with the samples. The digested samples were made up to volume and analyzed for the following elements:

Na and K: Flame emission.

Ca, Cu, Mg, Mn: Atomic absorption spectroscopy with an air-acetylene flame. $LaCl_3$ was added to the samples prior to the calcium analyses (1%), to avoid phosphate disturbances. Standard solutions were treated in the same manner (cf. Pawluk 1967).

P: According to Jackson (1958) using a mixture of ammonium-molybdate and ammoniumvanadate as a complex forming reagent.

S: Turbidimetry according to Blanchar et al. (1965).

Organic N + NH_4 : Ground samples (0.250 g in duplicate) were treated by wet digestion (conc. sulphuric acid and a catalyst consisting sulphates of copper and potassium. The digested samples were distilled and the ammonia liberated was collected in HCl, which was titrated with NaOH (0.05 M in both cases). The procedure is mainly according to Kjeldahl.

For further details concerning the chemical analyses, see Balsberg (1975).

6 RESULTS

6.1 Litter fall

6.1.1 Total amounts and distribution in time

In 1971 the normal time sequence of a temperate deciduous forest was followed with a small peak in May due to the leaf burst and subsequent shedding of bud scales, and a large one at the end of October when most of the leaf fall occurs. The pattern was essentially the same during 1972 but the autumn peak was slightly skewed towards the beginning of October, due to the activity of the D.p. larvae, resulting in the production of green leaf frass and faeces. 1973 had a totally different pattern as the peak of litter fall occurred already at the beginning of September and consisted mainly of faeces and green leaf frass, in that order of quantitative importance (Fig. 1-4).

Comparisons with Nihlgård (1972) are given in Tab. 1. The figures of the present investigation are given with 95 per cent confidence limits. All statistical calculations are performed according to Snedecor and Cochran (1967). Nihlgård's measurements were made during 1967-1969. According to the stand comparison in Tab. 1 the trees in the research plot of the present investigation were much more sparsely distributed ($120 \text{ trees} \cdot \text{ha}^{-1}$, against $240 \text{ trees} \cdot \text{ha}^{-1}$). This was due to a selective cutting performed by the land-owner during the winter of 1970-1971. Different tree densities and strong winds during 1967 and 1969 could be the explanations for the rather large discrepancy between the two investigations concerning total litter fall. The most relevant comparison can be made between the 1971- and 1967-69 data, as the forest was practically unaffected by D.p. larvae during these years. On the other hand, it can be seen from Tab. 2 that although there is a decreasing tendency from 1971 to 1973, the differences between the years are too small to be statistically significant at the 95 per cent level. Significance of differences between arithmetic means

are evaluated with the Student's t-test. According to Bray and Gorham (1964), a tentative mean value for annual litter fall in beech stands of Europe should be in the range of 3.4 ton.ha^{-1} , which is in agreement with the present investigation. Their compilations also show, that differences of annual litter fall due to tree density should be almost negligible within a wide range of density values, the leaf production of various stands being of approximately the same magnitude. There should however elapse some time from the date of cutting, until the remaining trees have adopted themselves to the relaxed competition for resources such as light, nutrients and water.

The leaf litter fall in the present investigation varies widely between the years, the differences being highly significant, even between 1971 and 1972.

6.1.2 Litter fall distribution in space

It was suspected that the litter fall of 1973 would be more unevenly distributed than normally, because of the quantitative dominance of faeces, as demonstrated by the figures of Tab. 2. The annual litterfall from individual traps was therefore related to distance and diameter at breast height (130 cm above the ground), of the four nearest trees (cf. Spain 1973). The best fit for 1973 and pooled data was obtained with the following second degree polynomial:

$$P : aw^2 + bw + c$$

P: annual litter fall in ton.ha^{-1}

$$w: \frac{\sum D}{\sum a + \sum 0.5D}$$

$\sum D$: the sum of breast height diameters of the four nearest trees in cm

$\sum a$: the sum of distances to the nearest four trees in m

$\sum 0.5D$: the sum of the average radii at breast height of the four nearest trees in m, introduced to include the distance from tree bole perimeter to tree centre in the tree distance figures.

a, b and c are equation parameters.

Tree diameters were incorporated in the function in order to account for variation in crown width (cf. Spain 1973).

Data are taken from a growth revision made during the winter of 1972, but although the breast height diameters increase annually, the relative figures for different trees should be comparable for a two-three-year period, especially when the average stand age (90 years) is taken into account. The polynomials for 1971, 1972, 1973 and the pooled litter production data for the whole period of investigation are shown in Fig. 5-8. Variance ratios (F-ratios) have been calculated, and are given in the figures. As the second degree polynomials of 1971 and 1972 are statistically non-significant, contrary to those of 1973 and the pooled data which are significant at the 95 per cent level, it is suggested that the litter distribution of 1973 is definitely more patchy than during the preceeding years, mainly because of the large dominance of faeces, which probably have a much lower surface/weight ratio than the leaves, and are thus concentrated in the vicinity of the trees. The statistical significance of the pooled data is mainly attributed to the large impact of the 1973 data. It can also be noted that although the F-ratios of 1971 and 1972 are non-significant there is an increasing tendency for the three years, which might indicate that the 1972 data are influenced by the faeces contribution to some extent. The increasing patchiness of litter fall has important implications on comparisons between the years. It may be expected for instance that a larger amount of litter traps would have revealed quantitative differences more clearly, but on the other hand increasing standard deviations and confidence intervals could often have an information value of their own.

6.2 Chemical data on litter fall and throughfall.

6.2.1 Plant nutrient fluxes in litter fall and throughfall

The throughfall flux is significantly higher for nitrogen, phosphorous and potassium in 1973 than in 1971 (Fig. 9-11, Tab. 3), which is attributed to leaching from faeces and injured leaves. Plant nutrient fluxes in leaf litter and "other" litter differ markedly within and between years for obvious reasons. Summation of the two litter fractions yields significantly higher phosphorous values in 1971. Nitrogen reveals the opposite trend, whereas no difference can be found for potassium. When litter and throughfall figures are added together it appears that the nitrogen and potassium fluxes are considerably higher in 1973. Phosphorous although not significantly increases slightly (Fig. 9-11, Tab. 3).

The fluxes of eight mineral elements including nitrogen in litter fall are shown in Tab. 4. The 1972 data are tentative to some extent as fluxes between April and August are estimated by multiplying 1972 weight data with appropriate concentration data from 1971. 21.5 per cent of the yearly litter fall calculated by dry weight occurs between 18/4 1972 and 31/8 in the same year. The faeces contribution is not obvious until September, which could mean that the chemical composition of spring and summer litter fall ought to be fairly comparable with the 1971 situation.

Redistribution of elements between leaf litter and "other" litter can be demonstrated for all elements, with increasing dominance of "other" litter in the order 1971, 1972 and 1973. Unfortunately a full evaluation of the 1972 data is not possible because of too few chemical analyses of throughfall precipitation. Most of the between-year differences between total litter and individual litter fractions are highly significant (Tab. 5).

A comparison between the 1972 and 1971 data reveals higher fluxes in total litter for all elements except

for sodium in 1972. The reasons for this are suggested to be:

- 1) The inclusion of larval faeces in 1972.
- 2) The leaf litter fall and the fall of "other" litter between 19/9 and 16/10 1972 make up 100.3 and 154 per cent respectively of the fall of the corresponding fractions between 16/10 and 2/11 the same year.

In 1971 the leaf litter fall between 23/9 and 14/10 is 53.1 per cent of that between 14/10 and 1/11. The corresponding figure for "other" litter is 109 per cent. The plant nutrient concentrations in leaf litter are generally higher in September than at the normal peak of leaf litter in October, at least as far as nitrogen, phosphorous and potassium are concerned (see below for further comments). This could definitely contribute to the higher figures of 1972. It should be admitted, however, that litter was sampled more intensively during 1972 and 1973 than during the first year of investigation. This has probably affected the potassium figures to some extent. Carlisle et al. (1966a) made a comparison of element concentrations between oak leaf litter collected at the end of autumn leaf fall and at weekly intervals. The only significant difference was found for potassium. On the other hand one should be aware of the fact that a rather large part of leaf litter fall in 1972 consisted of green leaf frass, which should raise the potassium figures although they still can be somewhat over-estimated.

Total amounts of plant nutrient elements in litter fall are higher in 1972 than in 1973 except for nitrogen. This should be due to the following facts:

- 1) Leaf litter including green leaf frass makes up but a tiny contribution to total litter fall in 1973.
- 2) Certain amounts could have accumulated in the larval bodies.
- 3) Substantial amounts should be found in the stand precipitation due to leaching from faeces and wounded leaves, which was actually confirmed for nitrogen, phosphorous and potassium.

The relative importance of any two litter fractions can be expressed as a ratio (the two litter fractions designated a and b):

$$\frac{\text{Plant nutrient content of litter fraction "a" in kg.ha}^{-1}.\text{year}^{-1}}{\text{"b" in kg.ha}^{-1}.\text{year}^{-1}} .$$

Values larger than 1.0 mean that the "a" fraction is relatively more important for the flux of plant nutrients than the "b" fraction, values less than 1.0, meaning the opposite. If concentration values are known it could be judged whether a high concentration could compensate for a low weight contribution and vice versa. Ratios have been calculated using the 1973 data. Acorns have been compared with bud scales as they made up comparable weight fractions that year (6.4 and 9.0% respectively). Leaf litter (17.0%) was compared with faeces (29.6%). The results can be seen in Tab. 6. The comparison reveals that the acorns could be assigned a larger importance than the bud scales for phosphorous and potassium. Leaf litter is more important than faeces as far as phosphorous is concerned, despite the much larger weight contribution of the latter fraction. A tentative explanation for this could be that phosphorous is easily leached from the faeces and/or a selective binding of this element in the larval tissues, provided of course that the phosphorous content of leaf litter is comparable with that of the leaf parts actually consumed, which ought to be the case as the fall of senescent leaves which occurred in October-December was almost negligible from a quantitative standpoint. At this time of the year surviving larvae have already pupated.

6.2.2 Relative plant nutrient concentrations in some litter fractions

Plant nutrient concentrations are given as mole percentage values for leaf litter and faeces in Fig. 12-16. Relative chemical composition for leaf litter is shown for the middle of September, the middle of October and late October in 1971, 1972

and 1973. Similar trends can be observed for the three years except for potassium, meaning that in principle the relative chemical composition on comparable occasions remains the same, at least if potassium is left out of the calculations. The relative composition of faeces from September 1972 and 1973 is shown in Fig.15. The similarity between the years is obvious. Furthermore no notable difference between leaves and faeces can be seen. Corresponding calculations have also been made for budscales and acorns of 1973 (Fig.16). Acorns seem to be enriched with respect to nitrogen, phosphorous and potassium in comparison with budscales, senescent leaves and faeces, which indicates the general phenomenon of a high nutritional value in reproductive tissues.

6.3 Stem growth analysis

Measurements of the annual growth increment were made on felled logs, emanating from trees which were defoliated during two consecutive years. The logs represented the lowest parts of the tree stems. Within this log group a random selection was made. The measurements were proceeded back to the growth increment of 1969 (Tab. 7). Arithmetic means with 95 per cent confidence intervals were calculated for the different years. The growth differences between the years were evaluated with a Student's t-test. The growth increment of 1973 is the smallest among the years studied (Tab. 7). Significant differences could only be found between 1973 and 1972 ($p = 0.01$) and between 1973 and 1969 ($p = 0.05$). There are two main problems in a growth analysis of this kind:

- 1) Growth variance is considerable in a tree population. A larger investigation material would therefore have been desirable.
- 2) It is often extremely difficult to assign a decreased growth increment to one specific environmental factor. Temperature regime and amounts of precipitation during the vegetation period are often of decisive importance.

Variations of these factors could therefore conceal the influence of other abiotic or biotic ones (cf. Rafes 1970).

Figures showing the incident rainfall during May-September and June 1971 - 1973 are given in Tab. 8. The May-September figures are fairly similar. On the other hand the incident rainfall in June 1973 is definitely lower than during the same month 1971 and 1972. This could probably have an impact on the photosynthetic activity of the leaves. The defoliation performed by the D.p. larvae occurs rather late during the vegetation period (from the end of July to September) and it is stated in the literature that the growth reduction caused by D.p. defoliation should be comparatively slight (cf. e.g. Rafes 1970). Furthermore no decrease of total net primary production was observed between the two growth revisions that were made within the research plot:

Winter 1972: $13.8 \pm 1.6 \text{ ton.ha}^{-1}.\text{year}^{-1}$.

Autumn 1974: $14.4 \pm 1.6 \text{ ton.ha}^{-1}.\text{year}^{-1}$.

7 DISCUSSION

7.1 Sources of error in the field sampling procedure

As stemflow has not been measured, the stand precipitation is clearly underestimated. According to Nihlgård (1971), stem flow makes up approximately 14% of the stand precipitation calculated as $\text{litre.m}^{-2}.\text{year}^{-1}$ and the amounts of nitrogen, phosphorous and potassium in stem flow should be 4.5, 9.0 and 24.4% of those in total stand precipitation. Calculations made by the present author using Nihlgård's data, show that the ratio between plant nutrient amounts in stemflow and throughfall increases markedly in late autumn when leaf fall is completed:

	N	P	K
Average ratio of the period May-early October 1968	0.077±0.057	0.116±0.058	0.249±0.139
given with ± one standard deviation			
Ratio of November the 12th, 1968:	0.289	1.049	0.636

These examples indicate that a larger part of the plant nutrient fluxes is allocated to the stem flow fraction when the leaf biomass is absent. The tendency ought to be the same during the defoliation caused by the D.p. larvae. One would expect the corresponding ratios in the present investigation to increase in a rather continuous manner during the July-September period 1973.

The distribution of water, i.e. the carrying substance, during 1971 and 1973, was studied by using a regression model, where interception defined as $(1 - \frac{\text{throughfall}}{\text{incident rainfall}})$ as the dependent variable, was plotted against the intensity of incident rainfall expressed as $\text{litre.m}^{-2}.\text{day}^{-1}$.

A significant least square linear regression was obtained for the 1971 data ($r = -0.676^{**}$; $n = 15$). This was not the

case for 1973 ($r = -0.291$; $n = 12$). Furthermore the interception was significantly lower during the latter year ($t = 2.83^{**}$, obtained from Student's t-test). The outcome of the previous discussion leads to the following conclusions:

- 1) The defoliation in 1973 decreased the interception calculated from throughfall data and made it independent of the incident rainfall intensity.
- 2) A proportionately larger amount of the plant nutrient fluxes was allocated to the stemflow.

There should be a relative underestimation of the plant nutrient fluxes in 1973, compared with those of 1971. This is especially important as far as potassium is concerned, according to the ratios previously presented.

Furthermore, Carlisle et al. (1967) give the following sequence for quantitative importance in the stemflow of oak trees: $K > P > N$. Other sources of error could be dust fall from within the forest and soil splash effects, both having an impact on the throughfall data. Furthermore, leaching from the litter traps between sampling occasions could be mentioned.

A stratified radial sampling around the tree stems could have given a better estimate of the contribution of larval skins and dead larvae to total litter fall.

Coarse branches have not been included in the sampling of litter fall. The contribution of this fraction is largely stochastic in nature and varies considerably in time and space (cf. Carlisle et al. 1966a, Gosz et al. 1972, Nihlgård 1972 among others), who report weight contribution figures ranging from 9.5 to 22.2% of total litter fall. The lowest figure emanates from Nihlgård's data and is therefore more applicable to the present investigation than the others. There is probably no reason to believe that coarse branch litter fall should be influenced by the defoliation. Therefore the years of investigation should be comparable in relative figures.

7.2 Final discussion

7.2.1 Plant nutrient cycling

Investigations dealing with total defoliation are rather few in number. This is especially the case as far as plant nutrient cycling is concerned. Carlisle et al. (1966a) report very low consumption figures. Reichle et al. (1973) have developed a model describing the consumption rates of *Liriodendron tulipifera* leaves under normal conditions. The contribution from green leaf frass to the plant nutrient fluxes in total litter fall is estimated to be 2, 7, 5.5 and 8.5 per cent for calcium, potassium, nitrogen and phosphorous respectively. Kimmins (1972) performed a defoliation experiment with *Pinus resinosa* trees, using *Neodiprion sertifer* as a leaf (needle) predator. ¹³⁴Cs was chosen as a model substance for potassium and was injected in the trees. The experimental design consisted of two defoliated trees and two control trees. The isotope flux between twig generations and in litter fall and throughfall was followed. One of the main conclusions was that leaching from the canopy made a most significant contribution to the flux in the defoliated trees followed by green leaf frass and senescent litter in decreasing order of importance.

The importance of leaching was also demonstrated in the present investigation. Kimmin's study should be valid for comparison purposes, although the two investigations deal with deciduous and conifer trees respectively. One might suspect that the leaching of potassium from the upper parts of the soil profile should increase during a calamity like the one in the present study, especially as the research area is situated on a light textured soil (clay content in the B horizon is approximately eight per cent dw).

On the other hand elements like nitrogen and phosphorous would be mineralized at a faster rate than normally and either taken up by the plant roots or immobilized by microorganisms. This assumption is due to the fact that larval faeces

make up a considerable part of the total litter fall and are most certainly enriched with bacteria from the larval guts. Bacterial enrichment processes of this kind play a most significant role during the ordinary mineralization processes in the soil (cf. e.g. Edwards et al. 1970).

7.2.2 Tree growth

The reduction of stem growth observed in 1973, could not be attributed to the consumption of photosynthetic biomass, but could as well be due to low amounts of precipitation in May and June. Stem growth reductions were reported by Sylvén (1943) in the same area after the peak of the D.p. population during 1941 and 1942. He does not, however, present any growth data nor any information about the amounts of precipitation during that period. In the literature survey made by Rafes (1970) it is stressed that the time of defoliation is of crucial importance for the magnitude of growth reduction. According to the mentioned author D.p. could be classified as a late summer - autumn insect and should thus have a minor importance for the total growth increment of a certain year. The effect is of course enhanced if the population peak is extended over more than one year. Rafes gives figures from oak forests in the USSR, saying that the impact of a large D.p. population on tree growth should be a reduction in the order of 0 and 25 per cent during the first and second year of a population peak respectively.

It has been argued that the trees could have a benefit from a leaf consumption that is not too extensive, mainly on the presumption that the turnover of important plant nutrients should proceed at a faster rate (cf. e.g. Rafes 1970, Reichle et al. 1973 and Kimmins 1972).

Furthermore a partial defoliation increases the penetration of sunlight to the lower parts of the tree canopy. At the same time the water transport from incident rainfall is increased. These factors could of course also be negative for the tree population, because of increased competition from

other species in the tree or fieldlayer.

A final comment should be made about the possibilities to get a detailed picture of the annual growth increment pattern. The average age of the tree population is in the range of 90 years. This means that the population has reached the upper asymptotic part of the following growth function: $B/P_N = f(t)$, where B and P_N stand for tree biomass and net annual productivity respectively, and t is the stand age (cf. Odum 1971). Deviations from a normal growth pattern in this range of the curve are difficult to reveal as can be seen from the net annual productivity data of 1972 and 1974 which were earlier referred to.

7.2.3 The regulatory mechanisms of the *Dasychira pudibunda* population. Some hypotheses to be tested

A tentative model was described earlier (Myers 1976), which to some extent explains the fluctuation in numbers of the D.p. population. It is still rather obscure, though, which factors that are governing the growth rate of the population. At low population numbers the food resource (beech leaves), cannot possibly be a limiting factor. Weather conditions during winter might however be of decisive importance as the pupae are mainly located in the litter layer, which makes them sensitive of fluctuations in temperature and humidity. A long-lasting and rather deep snow cover has a good temperature insulating effect. Such a situation was realized during winter 1972, when the snow cover lasted from the beginning of January to the end of March. The winter of 1973 was fairly mild however, mean monthly temperatures measured at a meteorological station 10 km from the research area, were +0.4, +2.0 and +4.4 during January, February and March respectively. Data about short-term temperature fluctuations are not available.

The surviving last instar individuals from 1972 were the parent generation for the larvae of 1973. A hypothesis that could explain the two-year population peak is the following one:

Much of the energy that was gained by the larval population of 1972 was transferred to the wintering pupae. Even if there were a high mortality of pupae during winter 1973, the absolute number of surviving individuals should still be rather high. The survivors could be expected to have fairly large energy reserves. As mating and egg-laying occur immediately after hatching (Sylvén 1943) a substantial fraction of these reserves is allocated into egg production.

The pronounced population decrease after 1973 is suggested to be a combination effect of the over-exploitation of the food resource and increased attacks from parasites and predators (cf. Heqvist 1946, Sylvén 1943, Myers 1976). Less food is available for each individual, which could make the population as a whole more susceptible of parasitism and predation.

The advantages and disadvantages of a wildly fluctuating population number are rather difficult to reveal. A low population number diminishes the probability of parasitism and predation, at the same time as the food resource is not limiting. On the other hand the chances of mating are rather low, which would cause a low amount of gene recombinations. This process is better realized in a large population, but on the other hand the probabilities of parasitism and predation increase.

The co-evolutionary pattern of the beech and D.p. populations should finally be considered. It is known that many plant species evolve chemical compounds in their leaf tissues, which render the leaves less attractable or even unpalatable for the predators (cf. e.g. compilations by Dethier 1970 and Whittaker and Feeny 1971). As the population peaks of D.p. seem to be rather rare events it is perhaps uncertain whether the beech has developed such substances against D.p. If this is not the case the irregularity of the D.p. population pattern could be of some advantage for both the insect and the plant population in question: A good availability of food resources at an average, combined with a low probability of severe leaf predation, respectively.

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	Tree density (trees.ha ⁻¹)	DBH (cm)	Height (m)	Basal area (m ² .ha ⁻¹)	Tree biomass (ton.ha ⁻¹)	Tree NPP (ton.ha ⁻¹ . year ⁻¹)
<u>Present study</u>						
Growth revision						
winter 1972,						
average values	120	49.7	29.8	24.0	322.3±39.6	13.8±1.6
Range		19.4-65.5	23.8-31.7			
Growth revision						
autumn 1974,						
average values	120	50.7	30.1	24.9	339.0±40.7	14.4±1.6
Range		19.8-65.7	24.1-32.0			
<u>Nihlgård (1972)</u>						
average values	240	39.0	25.0	31.4	375.0±17.0	17.3±0.5
Range		12.3-64.0	11.0-29.0			

Tab.1.
Stand data from the present study compared with those of Nihlgård (1972) from the same general area. Figures of tree biomass and tree NPP from 1972 and 1974 are based on DBH and height application data combined with allometric regressions given in Nihlgård (op.cit).
± refers to 95 per cent confidence interval.

	Present investigation		Nihlgård (1972)		
	1971-1972	1972-1973	1967	1968	1969
	28/4-18/4	18/4-15/3			
		15/3-19/12			
Leaves	3.01±0.13	2.58±0.13	3.48	3.72	3.52
Twigs	0.36±0.12	0.20±0.10	0.79	0.26	0.61
Other material	1.05±0.14	1.52±0.25	0.80	0.49	1.81
Total litter fall	4.42±0.22	4.30±0.22	5.07	4.47	5.94

Tab.2.

Litter fall figures obtained in the present study, compared with corresponding data in Nihlgård (1972), calculated as ton.ha^{-1} , (dw 85°C).

± refers to 95 per cent confidence interval.

	N	P	K
<u>1971</u>			
Leaves	36.1±1.6	2.71±0.12	7.95±0.34
"Other" litter	13.8±1.6	1.09±0.12	3.54±0.40
Total litter fall	49.9±2.3	3.80±0.17	11.49±0.52
Throughfall	4.43±0.13	0.27±0.06	9.12±0.49
Sum of litter fall and throughfall	54.3±2.3	4.07±0.18	20.6±0.8
<u>1973</u>			
Leaves	15.3±0.8	0.82±0.04	2.55±0.13
"Other" litter	43.7±6.6	1.99±0.30	8.70±1.31
Total litter fall	59.0±6.7	2.81±0.30	11.25±1.32
Throughfall	12.16±0.64	1.47±0.48	24.89±3.77
Sum of litter fall and throughfall	71.2±6.7	4.28±0.64	36.1±4.7
Leaves	***	***	***
"Other" litter	***	***	***
Total litter fall	*	***	ns
Throughfall	***	***	***
Sum of litter fall and throughfall	***	ns	***

Tab.3.

The fluxes of nitrogen, phosphorous and potassium in litter fall and throughfall precipitation expressed as $\text{kg} \cdot \text{ha}^{-1}$. Separate figures are given for leaves and "other" litter. $\pm$ refers to 95 per cent confidence interval.

*** - $p = 0.001$; ** - $p = 0.01$; * - $p = 0.05$; ns - no statistical significance.

Significance levels refer to comparisons between the years.

	P	S	Cu	Mn	Mg	Ca	Na	K	N
<u>1971</u>									
Leaves	2.71±0.12	2.85±0.12	10.81±0.81	5.52±0.24	3.29±0.14	19.20±0.83	1.90±0.08	7.95±0.34	36.1±1.6
"Other" litter	1.09±0.12	0.86±0.10	12.65±1.42	0.88±0.10	0.79±0.09	4.77±0.53	0.18±0.02	3.54±0.40	13.8±1.6
Total litter fall	3.80±0.17	3.71±0.16	31.5±1.6	6.40±0.26	4.08±0.17	24.0±1.0	2.08±0.08	11.5±0.5	49.9±2.3
<u>1972</u>									
Leaves	2.25±0.11	3.11±0.16	25.75±1.29	5.11±0.26	2.87±0.14	17.11±0.86	1.27±0.06	9.73±0.49	30.9±1.5
"Other" litter	1.62±0.28	1.57±0.27	24.22±4.17	1.93±0.33	1.50±0.26	8.52±1.47	0.42±0.07	6.47±1.11	24.9±4.3
Total litter fall	3.87±0.30	4.68±0.31	50.0±4.4	7.04±0.42	4.37±0.30	25.6±1.7	1.69±0.09	16.2±1.2	55.0±4.6
<u>1973</u>									
Leaves	0.82±0.04	0.81±0.04	11.30±0.58	1.19±0.06	0.91±0.05	5.24±0.27	0.20±0.01	2.55±0.13	16.2±0.08
"Other" litter	1.99±0.30	2.85±0.43	33.34±5.00	3.59±0.54	2.72±0.41	13.75±2.06	0.60±0.09	8.70±1.31	43.7±6.6
Total litter fall	2.81±0.30	3.66±0.43	44.6±5.0	4.78±0.54	3.63±0.41	19.0±2.1	0.80±0.09	11.3±1.3	59.9±6.7

Tab.4.

The fluxes of eight mineral elements and of nitrogen in litter fall during three consecutive years. Values are expressed as $\text{kg} \cdot \text{ha}^{-1}$, except for copper, ($\text{g} \cdot \text{ha}^{-1}$). Separate figures are given for leaves and "other" litter.
 * refers to 95 per cent confidence interval.

	1971-1972		1971-1973		1972-1973	
	Leaves	"Other" litter	Leaves	"Other" litter	Leaves	"Other" litter
P	***	***	***	***	***	ns
S	**	***	***	***	***	***
Cu	***	***	***	***	***	*
Mn	*	***	***	***	***	***
Mg	***	***	***	***	***	***
Ca	***	***	***	***	***	***
Na	***	***	***	***	***	*
K	***	***	***	***	***	*
N	***	***	***	***	***	***

	1971-1972		1971-1973		1972-1973	
	Total	litter	Total	litter	Total	litter
P	ns	***	***	***	***	***
S	***	***	ns	***	***	***
Cu	***	***	***	***	ns	***
Mn	**	***	***	***	***	***
Mg	ns	***	*	***	*	***
Ca	ns	***	***	***	***	***
Na	***	***	***	***	***	***
K	***	***	ns	***	***	***
N	*	***	*	***	ns	***

Tab.5.
The statistical significance of plant nutrient flux differences between years based on a Student's t-test. Data are taken from Tab.4.

	P	S	Cu	Mn	Mg	Ca	Na	K	N
Acorns/ Budscapes	1.17	0.67	0.83	0.75	1.05	0.64	0.53	1.86	0.96
Leaves/ Faeces	1.11	0.50	0.76	0.43	0.53	0.56	0.48	0.51	0.60

Tab.6.

Importance values of acorns, budscapes, leaves and faeces.

Definition:

Plant nutrient content of litter fraction "a", $(\text{kg} \cdot \text{ha}^{-1})$
 $\frac{\text{"a"}}{\text{"b"}}, \frac{\text{"a"}}{\text{"b"}}, \frac{\text{"a"}}{\text{"b"}}, (\text{kg} \cdot \text{ha}^{-1})$

Data are taken from 1973.

	1969	1970	1971	1972	1973
	Annual		growth	increment	
Log no.					
1	1.5	1.5	2.0	2.0	1.2
2	2.0	2.0	2.5	3.0	1.5
3	1.7	1.0	1.0	1.2	0.7
4	2.0	2.0	2.0	2.0	1.0
5	1.0	1.0	1.5	2.0	1.5
6	1.5	1.0	1.0	2.0	1.0
7	2.0	2.0	1.5	2.0	1.5
8	2.5	3.0	3.0	3.5	2.5
9	2.0	2.0	2.0	2.0	1.0
10	2.0	1.5	1.5	1.5	1.0
11	3.0	2.5	2.5	3.0	2.0
12	1.0	1.0	1.0	1.0	1.5
13	1.0	1.0	1.0	1.0	2.0
14	2.0	1.0	1.0	1.0	1.5
15	2.0	2.0	2.0	3.0	2.0
16	1.5	1.5	1.5	2.0	1.0
17	1.5	1.5	1.0	2.0	1.0
18	1.5	1.0	1.0	2.0	1.0
19	3.0	2.0	2.5	2.5	2.0
Average	1.8 *	1.6 ^{ns}	1.7 ^{ns}	2.0 **	1.4
95 percent					
conf. interval	±0.3	±0.3	±0.3	±0.4	±0.2

Tab.7.

Annual growth increment measured on felled logs, expressed in mm.

Year	Period	Liter.m ⁻²
1971	June	83.4
1971	May-September	260
1972	June	77.8
1972	May-September	320
1973	June	33.6
1973	May-September	291

Tab.8.

Incident rainfall in the Kongalund area during 1971-1973, expressed as litre.m⁻². Values are given for the vegetation period (May-September) and for the month of June.

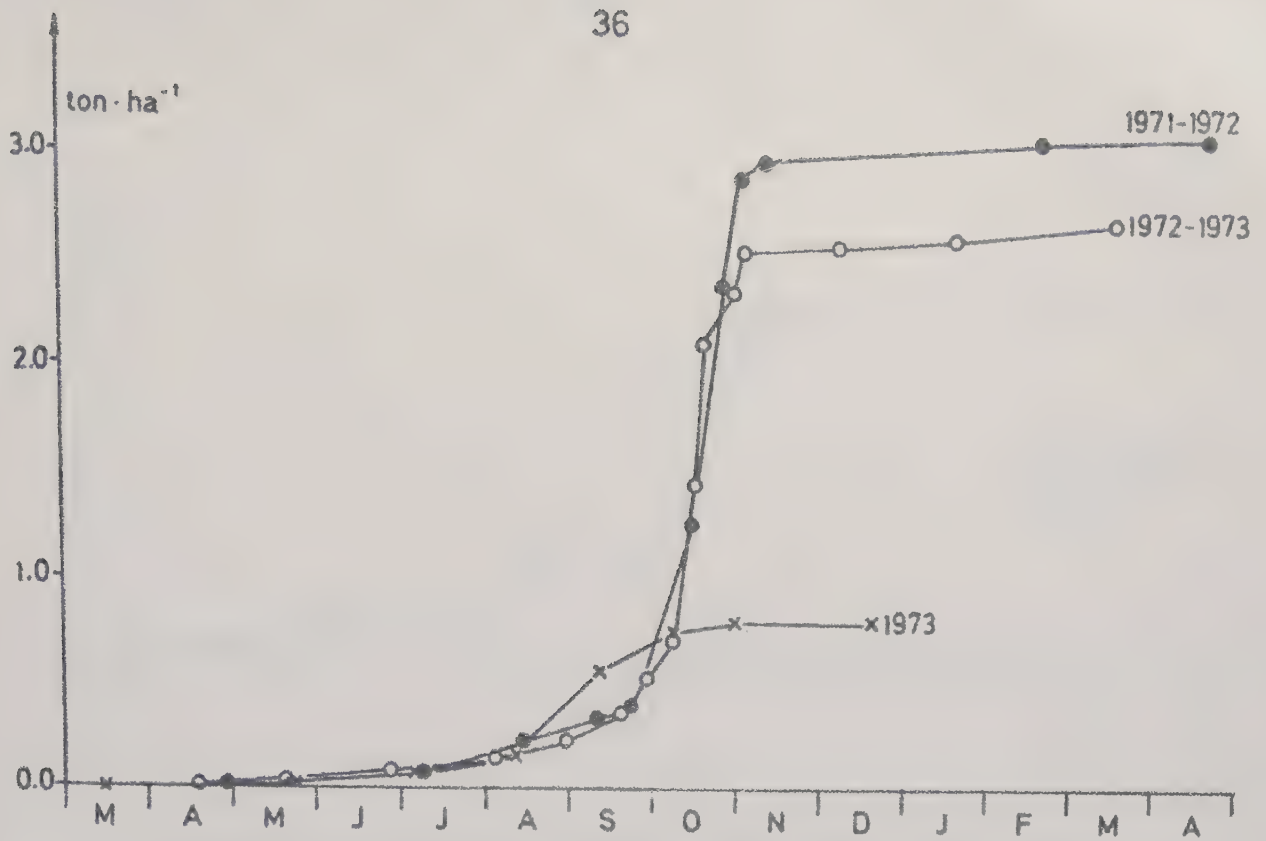


Fig. 1.

Cumulative curves of leaf litter fall. Figures are given as $\text{ton} \cdot \text{ha}^{-1}$. (dw 85°C).

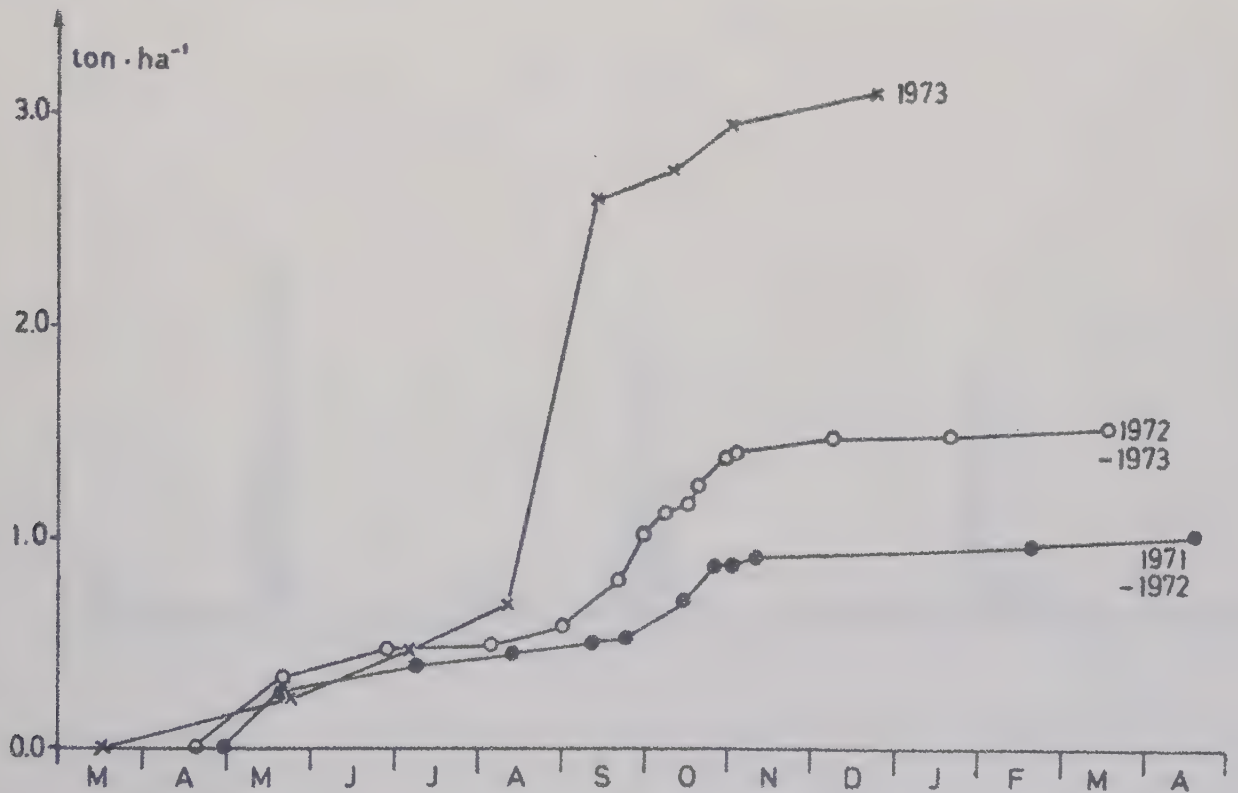


Fig. 2.

Cumulative curves of fall of "other" litter. Cf. Fig. 1.

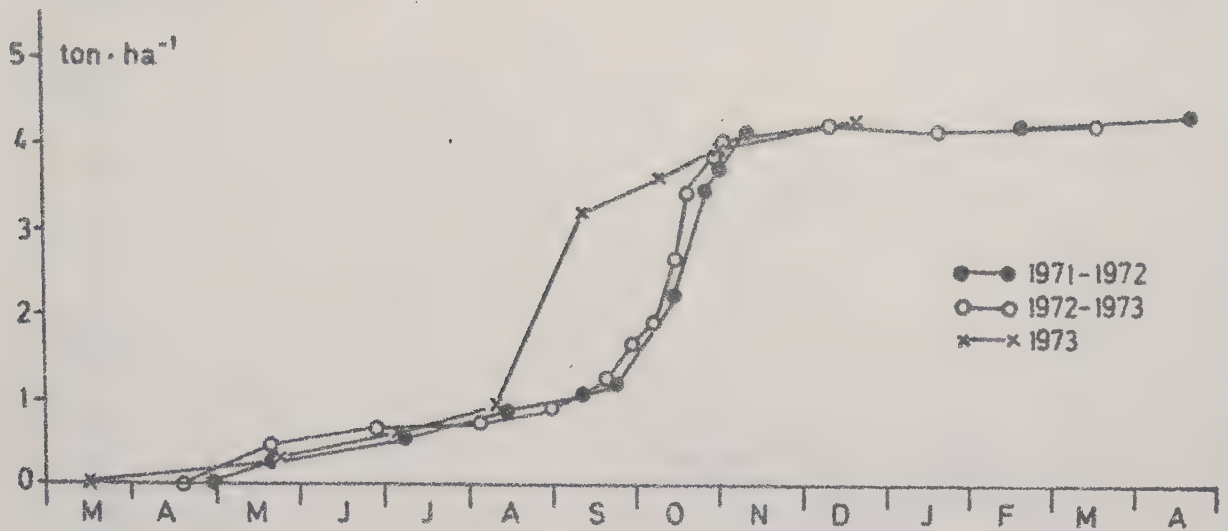


Fig. 3.

Cumulative curves of total litter fall. Cf. Fig. 1.

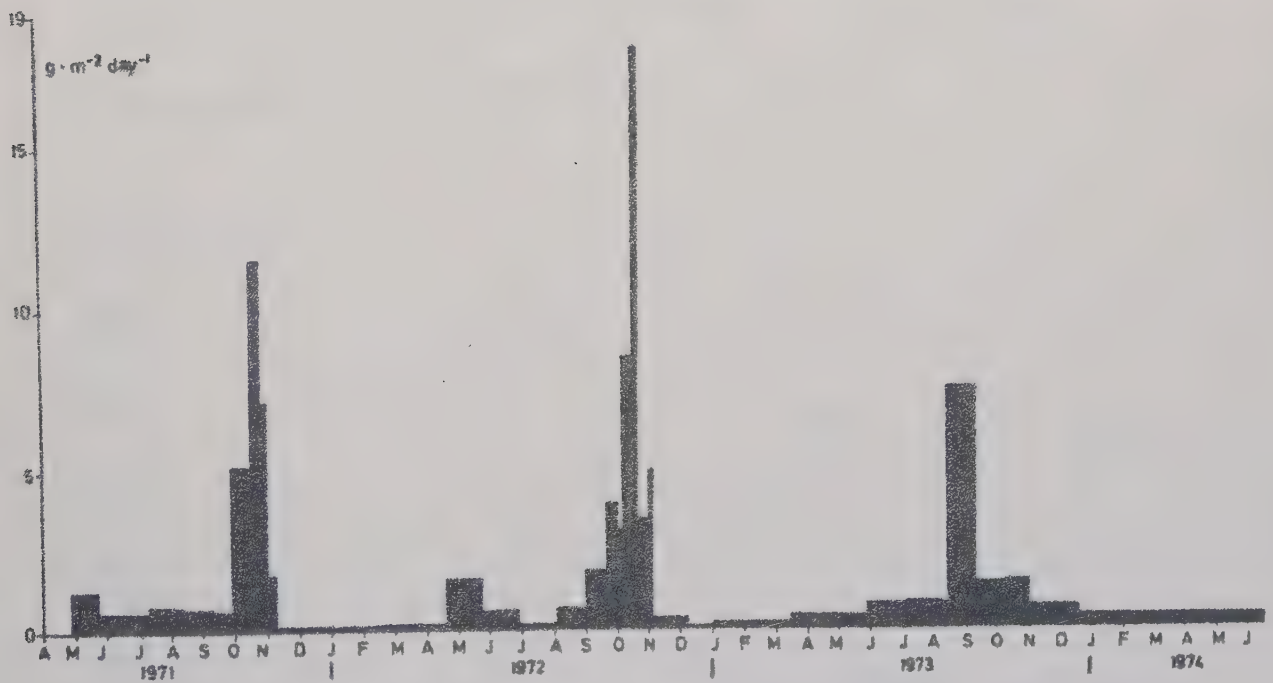


Fig. 4.

Rate of litter fall expressed as g · m⁻² · day⁻¹, (dw 85°C).

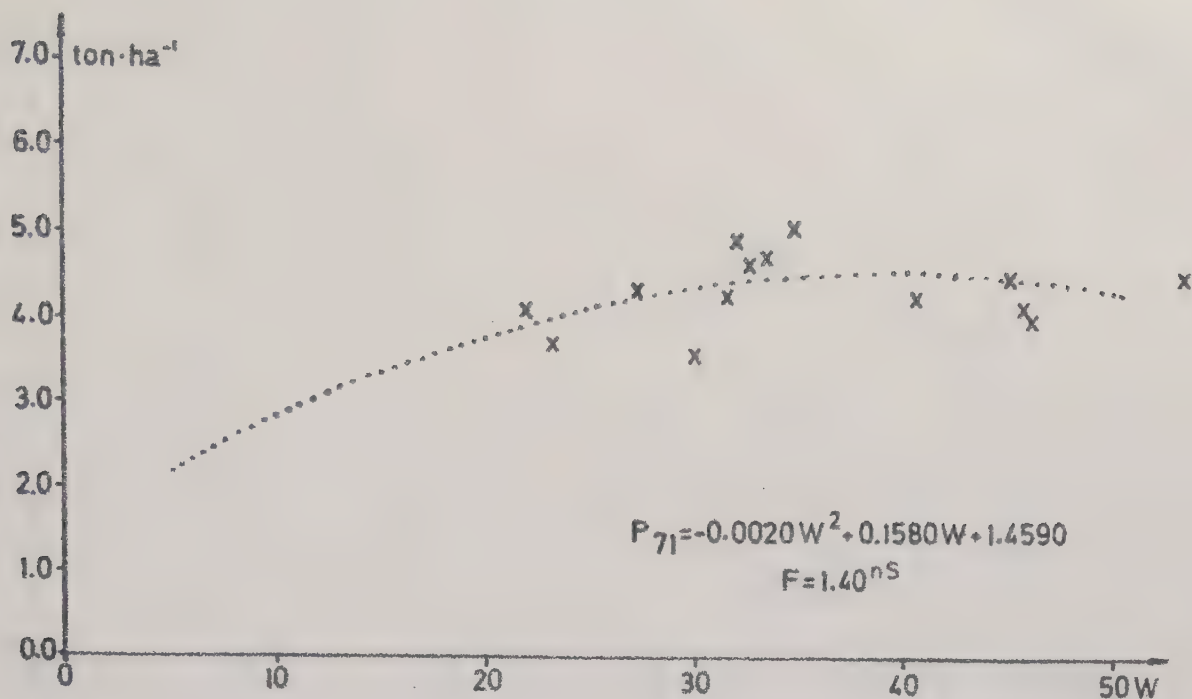


Fig. 5.

Litter fall (ton·ha⁻¹; dw 85°C) as a function of w , calculated for individual litter traps. $w = \frac{\Sigma D}{\Sigma a + \Sigma 0.5D}$;

See explanation in the text.

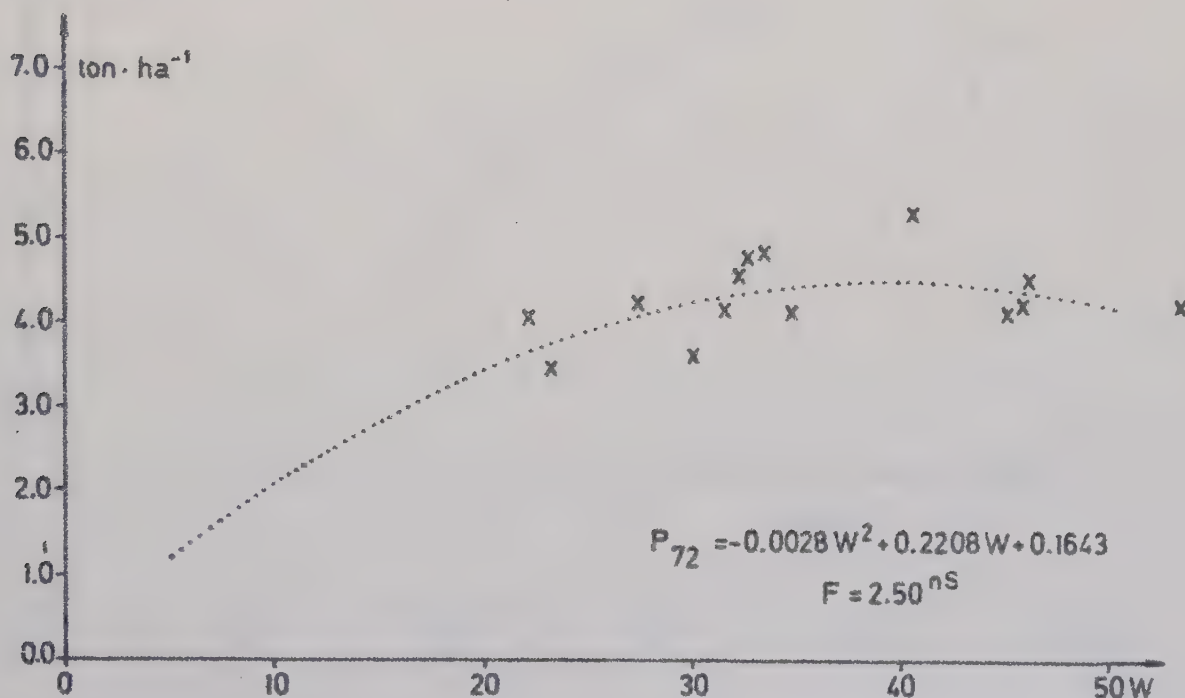


Fig. 6.

The same as in Fig. 5. Data from 1972.

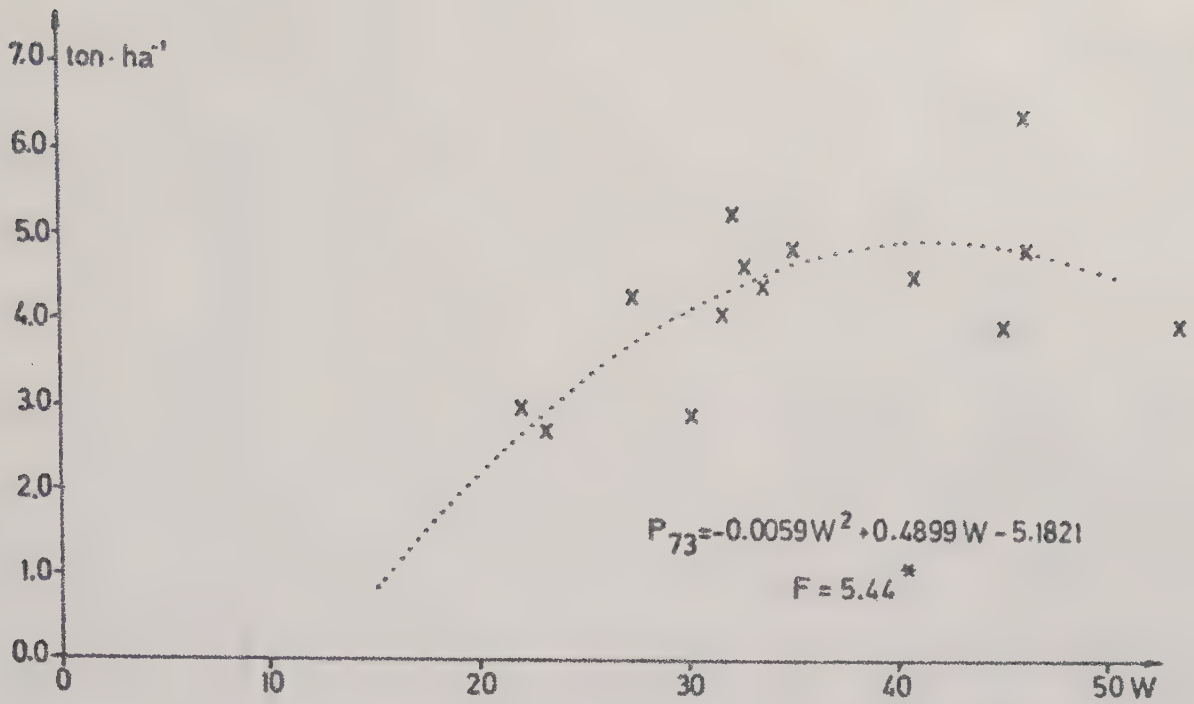


Fig. 7.

The same as in Fig. 5. Data from 1973.

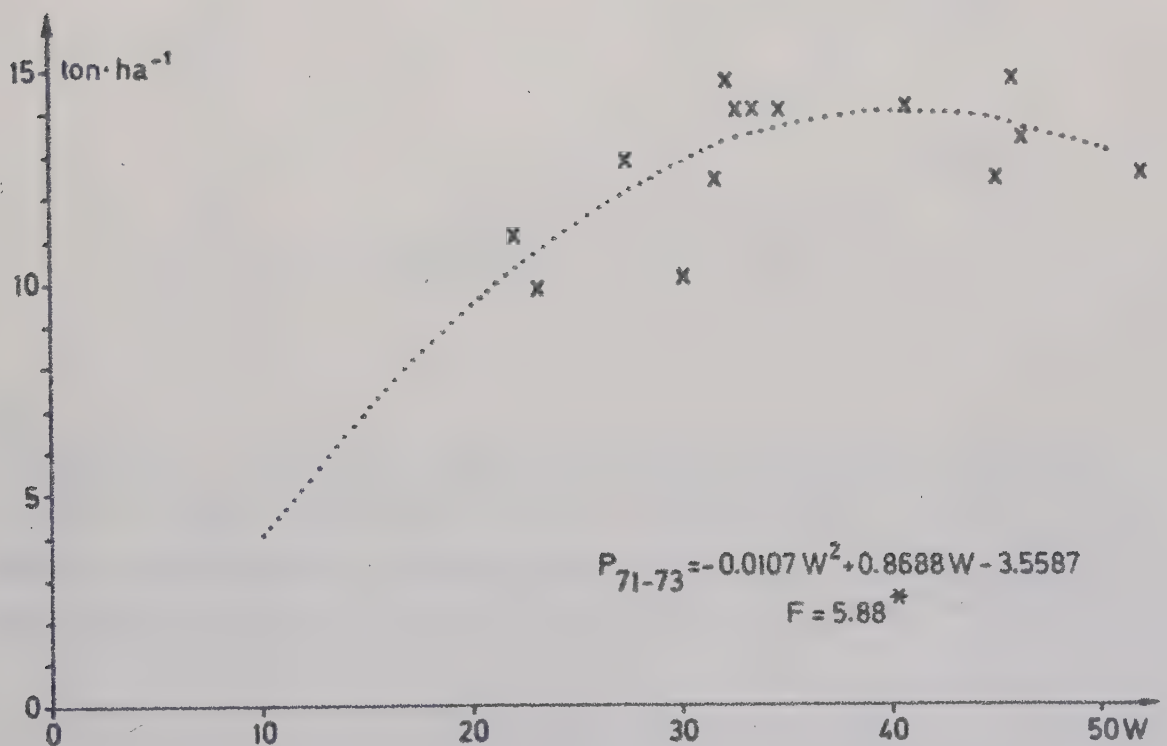


Fig. 8.

The same as in Fig. 5. Pooled data from 1971-1973.

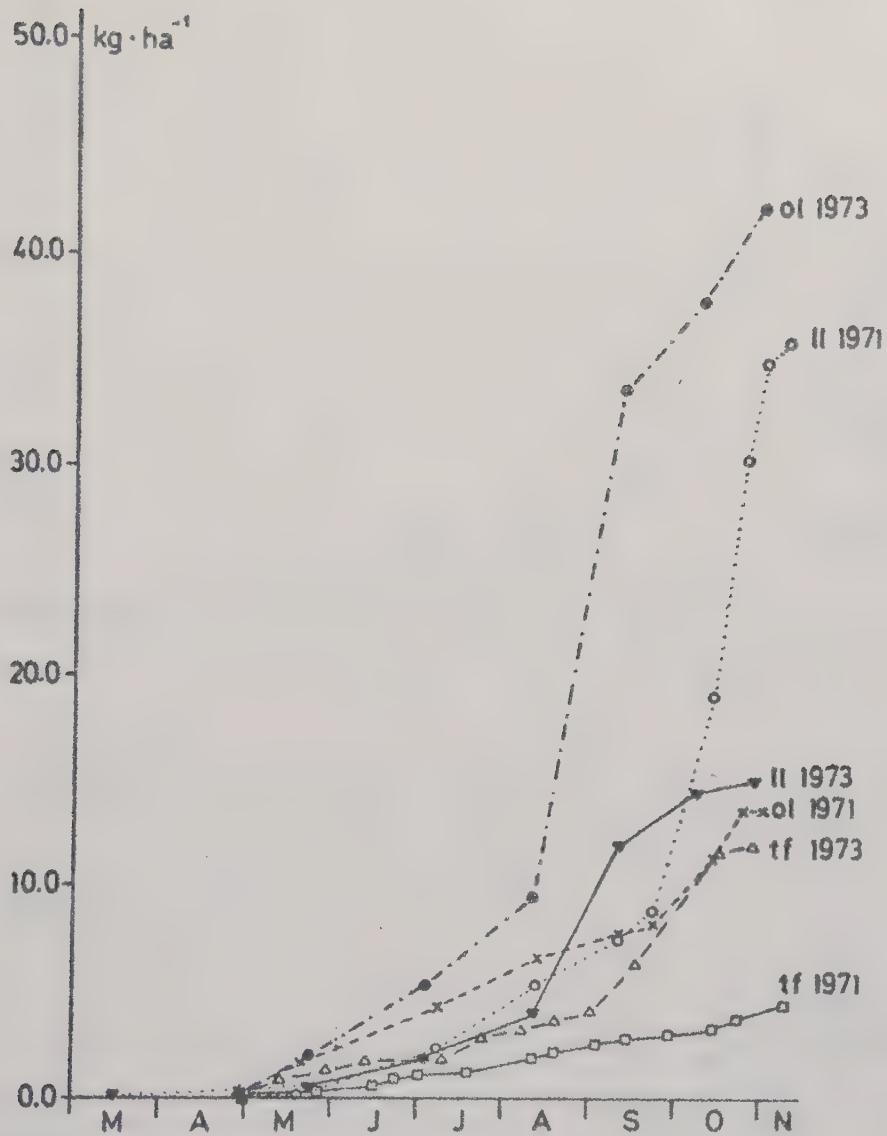


Fig. 9.

Cumulative curves showing the nitrogen input to the forest floor in leaf litter fall (ll), fall of "other" litter (ol) and in throughfall precipitation (tf) during the vegetation periods of 1971 and 1973. The figures are given as kg·ha⁻¹ (dw 85°C).

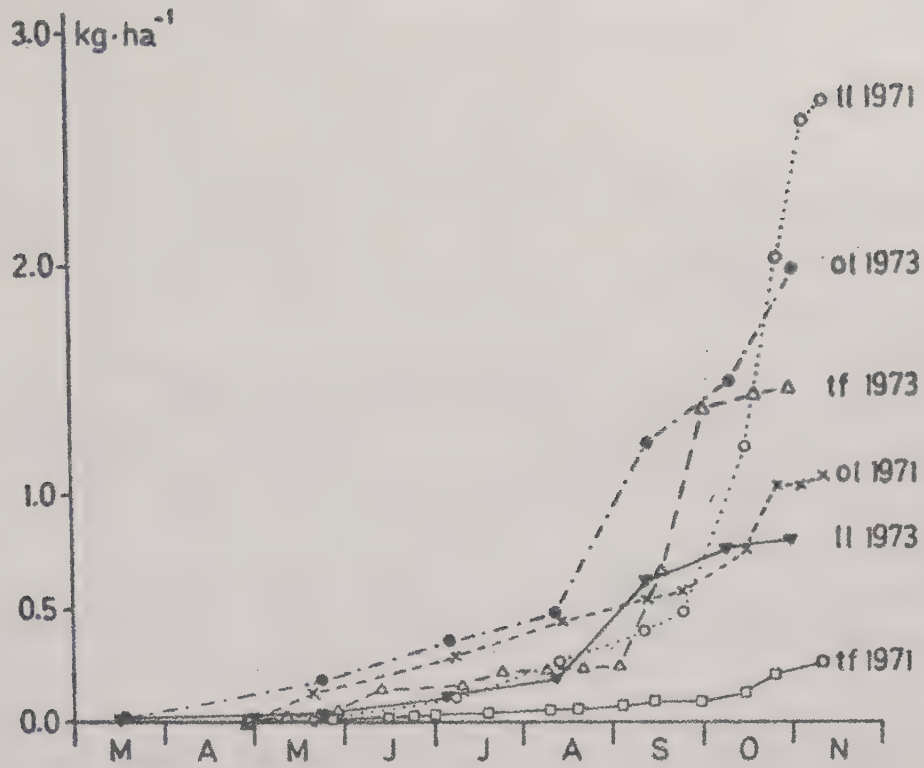


Fig. 10.

The same as in Fig. 9 shown for phosphorous.

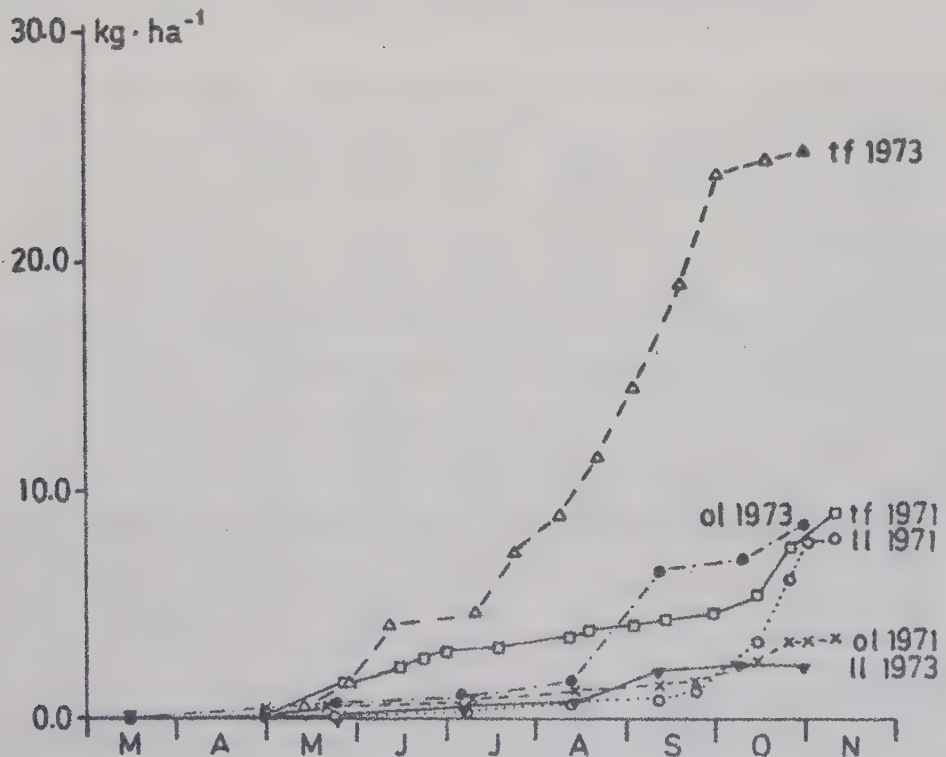


Fig. 11.

The same as in Fig. 9 shown for potassium.

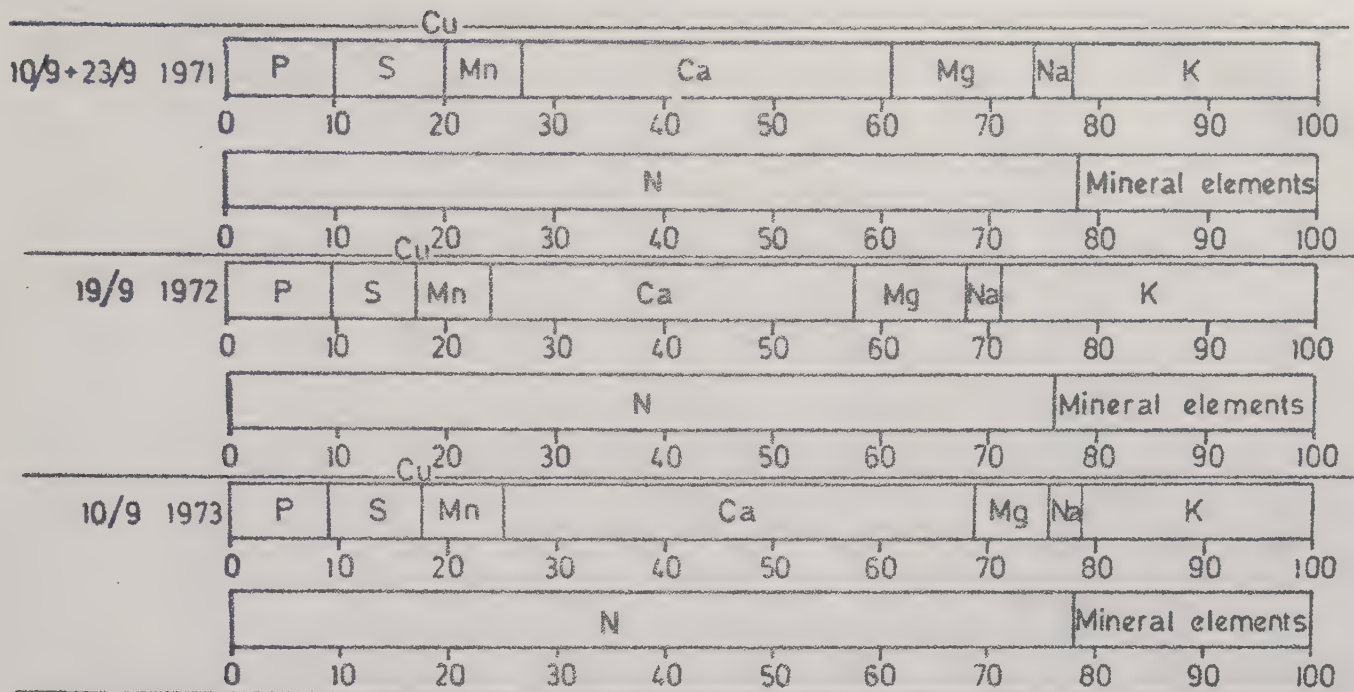


Fig. 12.

Relative plant nutrient concentrations in leaf litter in the middle of September during the three years of investigation. Mineral elements and nitrogen are treated separately for magnitude reasons. The way of calculation shown for phosphorous:

$$100 \frac{\text{phosphorous concentration (umoles.g}^{-1}\text{; dw 85}^{\circ}\text{C)}}{\text{sum of mineral element concentrations (umoles.g}^{-1}\text{; dw 85}^{\circ}\text{C)}}$$

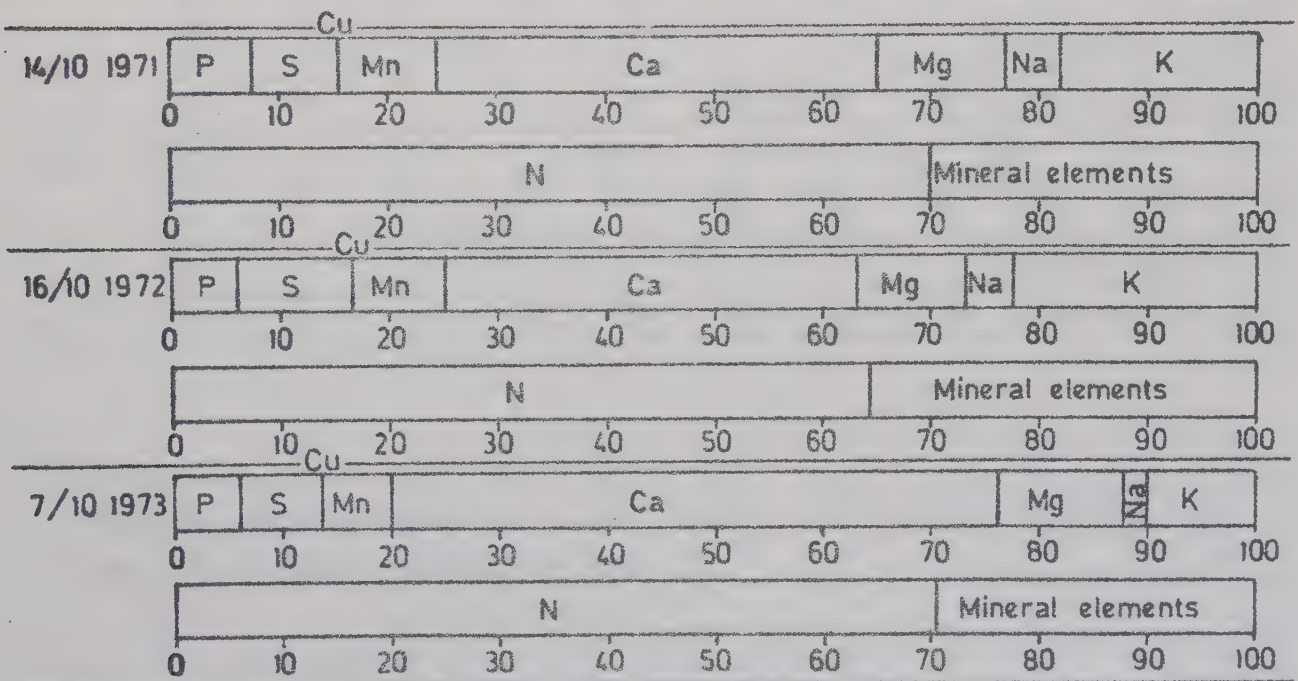


Fig. 13.

The same as in Fig. 12. Data from the former half of October during the three years of investigation.

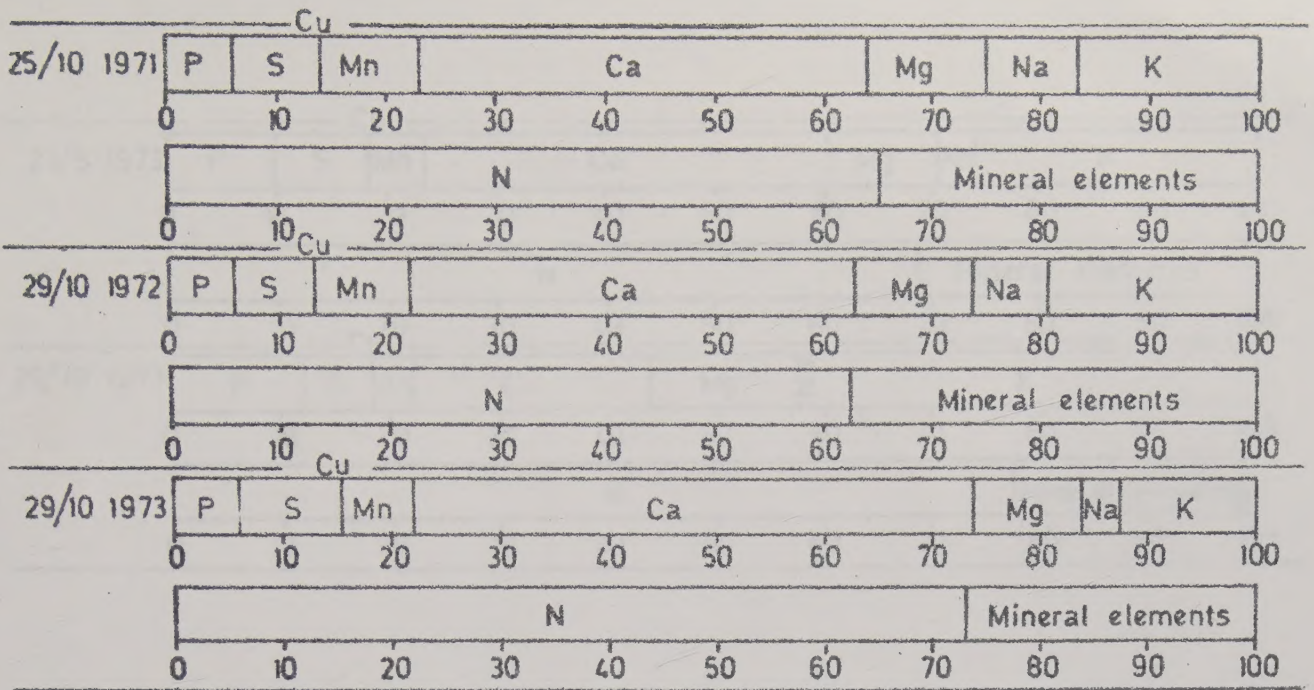


Fig. 14.

The same as in Fig. 12. Data from the latter half of October during the three years of investigation.

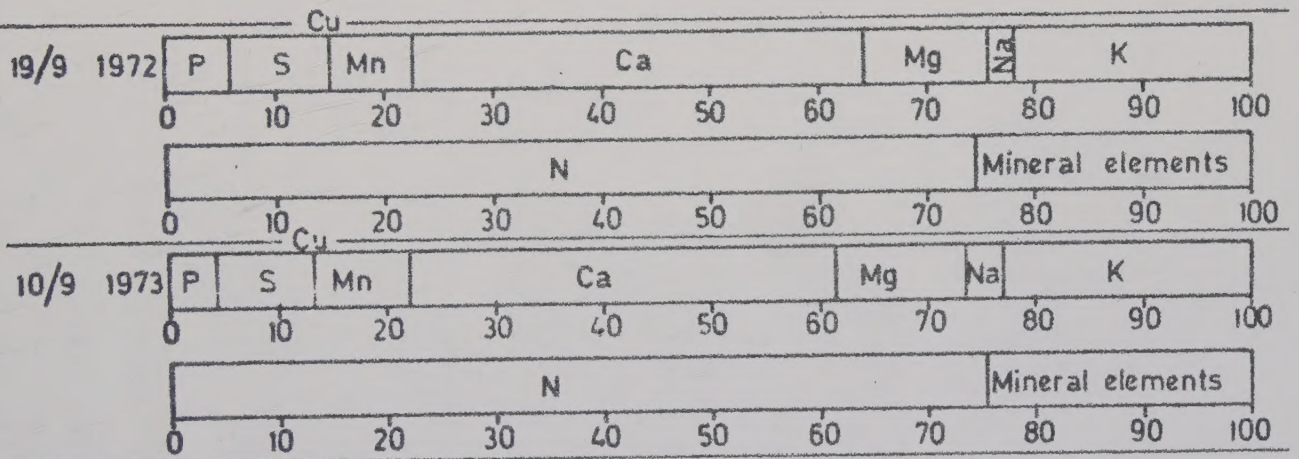


Fig. 15.

Faeces from the middle of September 1972 and 1973. The same way of calculation as in Fig. 12.

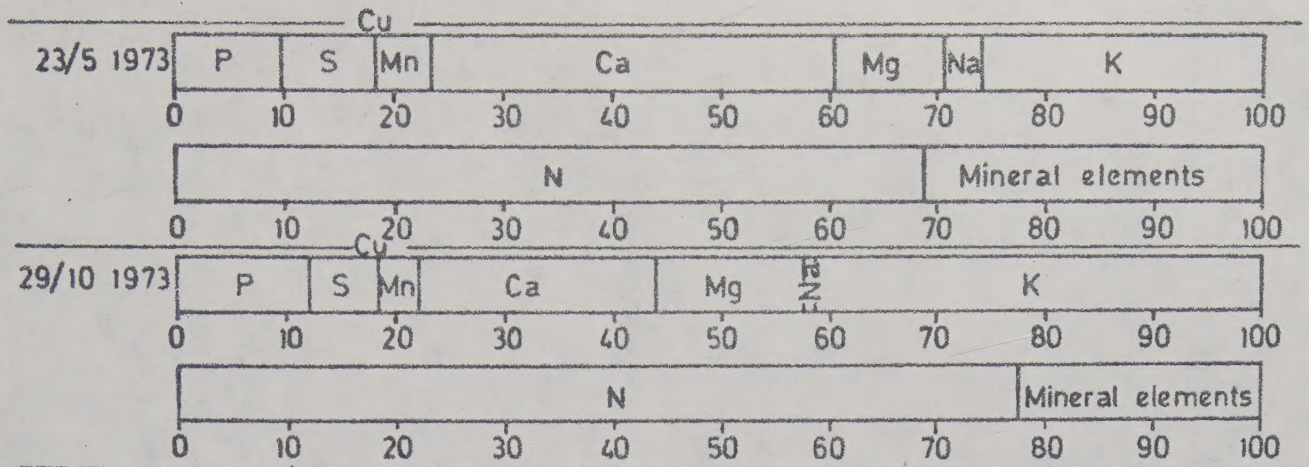


Fig. 16.

Acorns and budscales from October and May respectively, 1973. The same way of calculation as in Fig. 12.

